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A preliminary simulation model of individual and synergistic impacts of elephants and fire on the structure of semi-arid miombo woodlands in northwestern Zimbabwe

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Sustainable management of plant-herbivore systems requires an understanding of their long-term dynamics through modeling approaches. A preliminary simulation model was developed using STELLA to predict the impacts of elephants and fire on the structure of semi-arid miombo woodlands of north-western Zimbabwe. Elephants alone at a density of 0.27 km^{-2} will convert the woodland into coppice in 120 years due to resulting massive declines of large trees. The same result is achieved in only 10 years if elephant density is at 2 km^{-2}. The pattern remains similar with simultaneous application of fire once every 4.7 years with elephants at 0.27 km^{-2}. When elephants are culled at 30% whenever their densities reach 1 km^{-2}, the woodland does not degenerate into coppice despite fire occurrence once every 4.7 years. Therefore, elephants alone can degrade and maintain semi-arid miombo woodland into coppice, largely due to their damaging impacts on mature canopy trees and fire acts to speed up the process by suppression of an already low recruitment. Fire alone has a lesser influence on woodland structure than elephants because of low fuel loads due to heavy grazing and low grass production as a result of low rainfall and inherently poor soils in the area. A maximum elephant density of 0.1 km^{-2} is recommended to achieve equilibrium in the area.

Key words: Zimbabwe, Sengwa, STELLA, elephants, fire, miombo woodlands, simulation model.

INTRODUCTION

Spatial and temporal dynamics of plant communities are often strongly influenced by one or more types of disturbance events (Richards et al., 1999) of which fire and herbivory are two important determinants of semi-arid savannas. The impacts of these two determinants on vegetation largely depend on their frequency and timing of occurrence, as well as on the severity and the length of period of influence. The literature is awash with reports on the impacts of fire and elephant (*Loxodonta africana*

Blumenbach) herbivory on woodlands in general (Bond, 1993; Ribeiro, 2007; Valeix et al., 2011). The impacts of elephants and fire on semi-arid miombo woodlands were highlighted by, among others, Mapaure and Moe (2009) and Joseph (2012). Their influence in other savanna eco-systems such as Kalahari sand woodlands have also been reported (Holdo, 2007; Gambiza, 2001). The ability to predict the long-term impacts of fire and herbivory on the structure and composition of ecosystems and how

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ecosystems may respond to given levels of impacts should be an important consideration in ecosystem management. In semi-arid ecosystems, complex interactions among species, disturbance events, and unpredictable and low rainfall, make it difficult to assess probabilities and time scales of vegetation changes (Wiegand and Milton, 1996), making it a challenge to manage these ecosystems on a sustainable basis. In such situations, modelling becomes an essential approach which gives insights and understanding of future dynamics of ecosystems. In addition to exploring the long-term effects of disturbance factors on vegetation change over time, models also help in directing management strategies and decision-making with respect to fire and grazing/browsing management. Models come in various forms, including deterministic (in which relationships are fixed) and stochastic (in which parameters can vary), the latter being more appropriate for dynamic systems (Baxter and Getz, 2005; Taylor and Karlin, 1998).

In the last few decades, modelling has become a common approach to predict disturbance-induced vegetation change. Comparatively, more work has been done on modelling dynamics of moist forests and related ecosystems than on arid and semi-arid ecosystems. Rangeland dynamics are generally described with respect to the Clementsian concepts of single equilibrium (Clements, 1916) or state-and-transition model based on non-equilibrium dynamics (Westoby et al., 1989). The state-and-transition model holds that the transition of vegetation from one state to another is triggered by external shocks, and management regime is thought to alter the sensitivity of the rangeland to these shocks (Westoby et al., 1989; Perrings and Walker, 1997). Most current range dynamics models are constructed on the basis of the state-and-transition model. This approach allows inclusion of spatial variations and dynamics, event-driven changes, lag effects and thresholds of events (Walker, 1993). This approach is better in improving our understanding of dynamic ecosystems where functional processes may be quite complex.

In tropical savannas, a number of recent studies attempted to model the effects of grazing and/or fires on ecosystem dynamics. Pivello and Coutinho (1996) developed a predictive qualitative model on successional trends in Brazilian savannas under the influence of fire, grazing, wood cutting, drought, frost and weed invasion. Pivello and Norton (1996) developed an expert system with an ability to deal with qualitative information and recommended prescribed fire procedures accordingly for Brazilian savannas. Caughley (1976) developed a model on dynamics of *Colophospermum mopane* woodlands under the impacts of elephants in the Luangwa Valley, Zambia, in which he predicted a stable-limits cycle with a periodicity of 200 years. Caughley (1976) model was, however, recently doubted as unlikely (Mapaure and Mhlanga, 1998; Duffy et al., 1999). Predictions of miombo

woodland dynamics under the influence of various disturbance factors have largely been presented in conceptual models in the form of flow diagrams. These conceptual models were mainly based on observations in long-term experiments within the southern African region, some of which dealt with influences of fire (Trapnell, 1959) and regeneration after clearing (Robertson, 1984).

Frost (1996) indicated that shifts in the state of miombo from a woodland state to shrubland or grassland were driven by wood-clearing, elephants and fire. Such a situation was becoming evident in some areas of Sengwa Wildlife Research Area (SWRA) (Mapaure, 2001), the study site for this research. Starfield et al. (1993) developed a frame-based model to investigate interactions among rainfall, elephants and fire, which they applied to miombo woodlands of western Zimbabwe. Further to this, Desanker and Prentice (1994) and Desanker (1996) developed a computer model called MIOMBO on miombo woodland dynamics, with particular application to Malawian woodlands. Their model was based on individual-tree gap models and included a drought routine. Light conditions were modelled as the only restriction for a species to establish. This is an over simplification of ecosystem processes. Much more recently, Baxter and Getz (2005) used a grid-based model to evaluate elephant impacts on savanna dynamics in Kruger National Park, South Africa. Their model constitutes what could be considered a much more realistic representation of ecosystem dynamics under the influence of elephants and fire. However, most of the models discussed earlier largely dealt with structural dynamics rather than species composition, the latter being more challenging to model.

The need to model miombo woodlands dynamics has long been recognised by the Miombo Network. The Miombo network comprises an international network of researchers which aims to understand how land use practices affect land cover and ecosystem processes in miombo ecosystems of central, eastern and southern Africa. They also aim to predict the effects of global change on land use dynamics, structure and function of miombo ecosystems. One of their objectives is 'to develop a predictive understanding of miombo woodland structure and functioning' (Desanker et al., 1997).

The objective of this study was, therefore, to build a simple preliminary simulation model which best describes changes in the structure of semi-arid miombo woodland under the influence of elephant herbivory and fire. Modelling was done for structure because Baxter and Getz (2005) noted that even in cases where elephant impacts on woody plants may not significantly affect species composition, the structure is usually considerably altered. Also, the STELLA modelling platform used was developed to deal with changes in stocks. It is hoped that this will help decision-makers and resource managers to improve their elephant and fire management programmes in the miombo ecoregion in East and southern Africa.
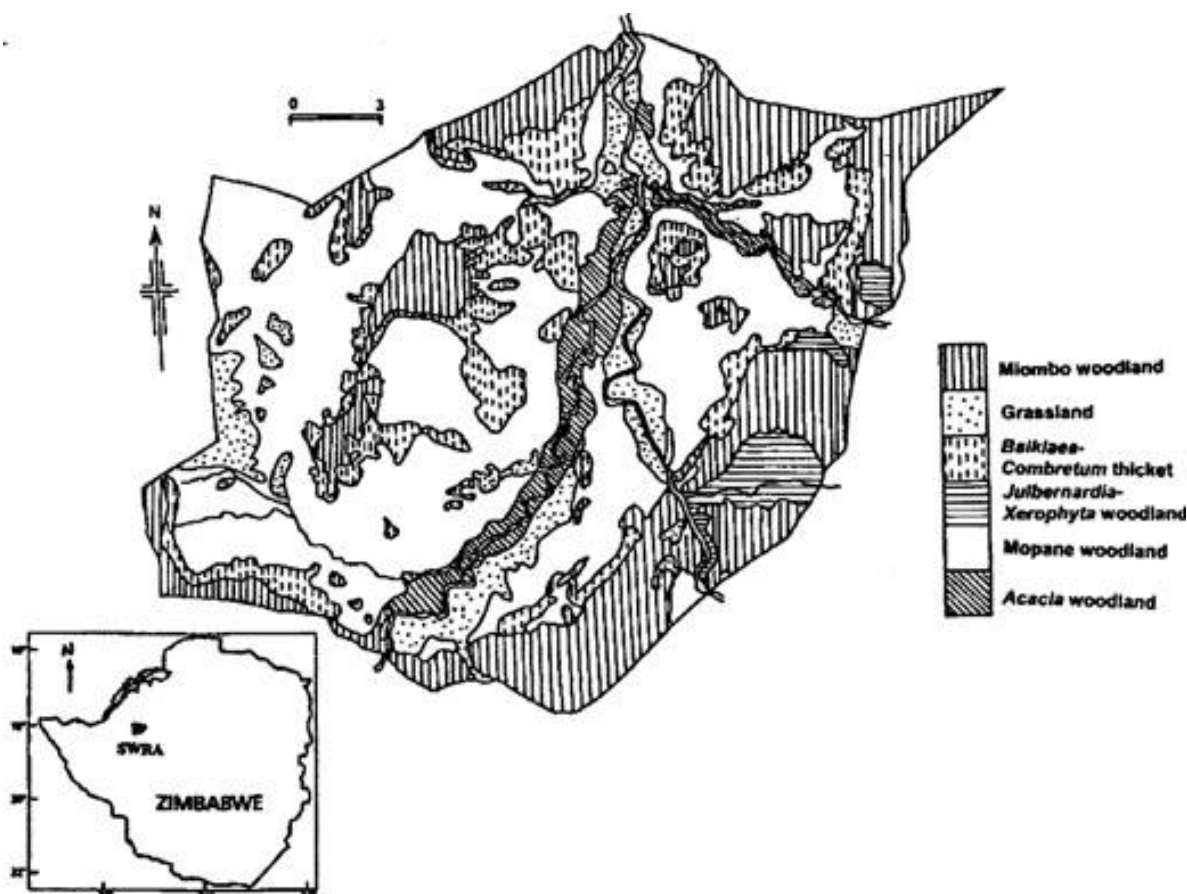
Figure 1. A map showing the location of Sengwa Wildlife Research Area (SWRA) in Zimbabwe and a detailed map of SWRA showing the major vegetation types in the area.

MATERIALS AND METHODS

Study area

This model was calibrated and based on data collected from various studies done by the author and other researchers (Anderson and Walker, 1974; Coulson, 1996; Craig, 1983; Guy, 1989; Mapaure, 2001; Mapaure and Campbell, 2002; Mapaure and Moe, 2009; Mapaure et al., 2009) in SWRA, north-western Zimbabwe (Figure 1). SWRA lies between 28° 03' and 28° 20' E and 18° 01' and 18° 13' S, covering an area of 373 km². It is bounded by communal lands on all but the northern side, where it shares a border with Chirisa Safari Area, a state protected hunting area. SWRA experiences three climatic seasons: a hot wet period from November to April, a cool dry period from May to July and a hot dry period from August to October. Mean annual rainfall is 642 mm while mean annual temperature is 24°C. October is the hottest month and July is the coldest. Altitude varies from 808 to 1043 m. The area is drained by three major rivers, the Sengwa, Manyoni and Lutope. Two main soil types occur, one formed on sandstones of the Escarpment Grits and another formed on mudstones (Selibas, 1974; Bennett et al., 1983). The vegetation is generally deciduous *Brachystegia–Julbernardia* (miombo) woodland on sandy soils and dry early deciduous woodland dominated by *Colophospermum mopane* on the lower heavier soils.

Other vegetation types are riverine *Acacia* woodlands and mixed

Combretum thickets on sands. These habitats are home to a diverse large mammal community of seven species of large carnivores and eighteen species of large herbivores (Cumming, 1983).

Model description

The model was developed using STELLA (High Performance Systems, 1996). STELLA is an icon-based program which allows both graphical and tabular outputs (Blankenship et al., 1995). It is an object-oriented programming language designed specifically for modelling dynamic systems (Costanza and Gottlieb, 1998; Costanza et al., 1998). Once a structural diagram has been completed using the icons, STELLA can write the equations internally in the form of first-order difference equations and provides a list of rate variables and auxiliary variables necessary for mathematical formulation (Pan and Raynal, 1995). STELLA is recommended as an excellent modelling tool and provides a potential to break new ground for simulating biologically complex systems (Costanza, 1987; Hannon and Ruth, 1997). The model simulates the effects of fire and elephants on woody plants. Fire regime is regulated through grass biomass production; itself is a function of rainfall patterns. By varying the rainfall seasonal patterns and grass biomass production, the fire intensity and frequency would change accordingly. These factors, in turn influence recruitment of shrubs, saplings and seedlings into small and large tree classes. The possibility of the

woodland shifting into a coppice woodland state was also built into the model. Sets of rules were defined to control these dynamic possibilities. The model was calibrated for SWRA using data from the present study as well as other literature sources from similar or comparable ecosystems, particularly Campbell (1996), Kundlande et al. (2000), Mapaure and Mhlanga (1998), Campbell et al. (1996), Gambiza et al. (2008), Mapaure et al. (2009), Mapaure (2001) and Mapaure and Moe (2009). The model can be modified and adapted for other semi-arid systems such as teak woodlands on poor sandy soils by altering relevant parameters on rainfall, grass biomass production, recruitment rates, maximum tree densities and probabilities of fire occurence.

The model consists of five interactive sub-models covering rainfall, grass, trees, fire and elephants. Parameters used, assumptions and sources of data are given under each sub-model. Diagrammatic representations of the different sub-models and the details of the parameters used (including justifications for the values used in the calculations and their sources) are given in the Appendix.

Rainfall sub-model

This sub-model generates the annual rainfall, which influences grass production. Rainfall was generated using the long-term mean annual rainfall for SWRA, the standard deviation of the mean and the sine wave function to simulate decade-scale fluctuations in rainfall around the long term average. The long-term period was set at 20 years as this broadly corresponds to the observed pattern of rainfall in southern Africa where there is an 18 to 20 year cycle comprising approximately 9 to 10 years above average rainfall alternating with a corresponding period of below average rainfall (Tyson, 1986). Recent changes in rainfall patterns due to climatic change were not included in the model due to their stochastic nature and inapplicability of the Global Circulation Models on local-specific events (IPCC, 2007). However, it may be possible to build this in the model by inclusion of carefully-thought out randomization climatic change generator.

Grass sub-model

This sub-model simulates grass biomass production; hence, grass fuel load. Grass production was calculated using regression equations relating production to rainfall in savannas (Dye and Spear, 1982) and shading by the tree canopy (Robertson, 1984; Frost, 1996). One millimetre of rain was assumed to produce 2 kg dry matter (DM) ha^{-1} yr^{-1} on cleared areas on sandy soils (Dye and Spear, 1982) while 1 mm of rain produces 1 kg DM ha^{-1} yr^{-1} under a high woody vegetation canopy cover (Frost, 1996). Fuel load was simulated as a function of grass growth rate, grass production, grazing rate, proportions of grass burnt off and grass decay. Successive years of above-average rainfall may result in the accumulation of grass fuel loads. Processes reducing grass biomass are decomposition, burning and grazing. Grass decay was estimated using a decomposition constant of 0.88 yr^{-1} for grass litter. It was estimated that the proportion of grass removed by herbivores was about 15% per annum, since the stocking rates of multi-species systems of wild herbivores were tricky to estimate compared to livestock production systems (Noy-Meir, 1981).

Fire sub-model

The occurrence of fires is simulated as a function of time-since-the-last fire and the probability of a fire spreading (a function of grass biomass). Trollope (1993) found out that fire only spreads in savannas when grass fuel loads were greater than 1000 kg DM ha^{-1}, though Rushworth (1975) earlier reported that fires could spread when the fuel load was as low as 800 kg DM ha^{-1} but it is noted that such fires did not cause top-kill of shrubs (Gambiza et al., 2000). The fire spread constant was therefore set at a grass biomass of 800 kg DM ha^{-2}. Natural fire was calculated as a random event determined by the probability of ignition. The probability of ignition was calculated as a function of the ignition constant and time-since-last fire; hence, the ignition constant was set at 0.3.

Elephant sub-model

This sub-model simulates densities of elephants in the area. The numbers of elephants at any one time is a function of additions through immigration and births, and subtractions due to culling, emigration and natural mortality. Immigration and births constitute natural increase. A natural rate of increase of 5% per annum in most elephant populations was reported by Cumming et al. (1997), a figure similar to that reported from Kenya (Armbruster and Lande, 1993). Between 1965 and 1979, elephant populations in SWRA increased at a rate of 4.19% per annum (Gibson, 1983). Therefore, a natural rate of increase (r) of 0.05 (that is, 5%) was used in the model and the growth rate was described by the logistic equation whose upper limit was set at 1500 elephants, limited by vegetation availability. Natural mortality of elephants in the Sebungwe was reportedly very low (Craig, 1996). Natural mortality was, therefore, set at 2% per annum, a mean of several values for SWRA given by Department of National Parks and Wildlife Management (1996). Poaching and animals killed through problem animal control were included in the culling variable, and this can be set by management. Both population increase and mortality are functions of the current population numbers, the base of which was set at 100, since the maximum recommended number for SWRA was 250 (Guy, 1989).

To simplify issues of differential use of habitats by elephants (with respect to availability of favoured species, extent of habitat relative to other habitats, proximity to water sources by elephants, spatial heterogeneity of food sources and variations in seasonality of elephant occupancy (including local migrations due to hunting disturbances during the hunting season), it was assumed that miombo woodland was the most available habitat for elephants at all times.

Tree sub-model

Woody vegetation was divided into four size classes representing shrubs (<3 m in height), small trees (3 to 5 m in height), large trees (>5 m in height), and coppice (converted trees and other elephant-and/or fire-suppressed trees). Transitions among size classes were set as a function of mortality, the proportion of individuals escaping a fire and growth rates of the respective strata. The current relative proportions of shrubs, small trees and shrubs in SWRA were used as base values for the model. Recruitment of individuals into the shrub layer was from seedlings whose establishment success is a function of grass biomass (incorporating competitive interactions between the two components). Elephants were assumed not to have any effect on shrubs but on small, large and coppice trees. Tree death was modelled as either natural or elephant induced while that of shrubs was either fire-caused or natural. The woodland was set to convert to coppice only when elephant density exceeded 2 km^{-2}. Reversions of small trees due to fire augmented numbers of shrubs but reversions of large trees due to elephants resulted in coppice woodland. Some of these dynamics are informed by Frost (1996).

Simulations

All simulations were run for a period of 200 years. This period was chosen because Caughley (1976) had indicated that equilibrium conditions between elephants and woodlands may be reached
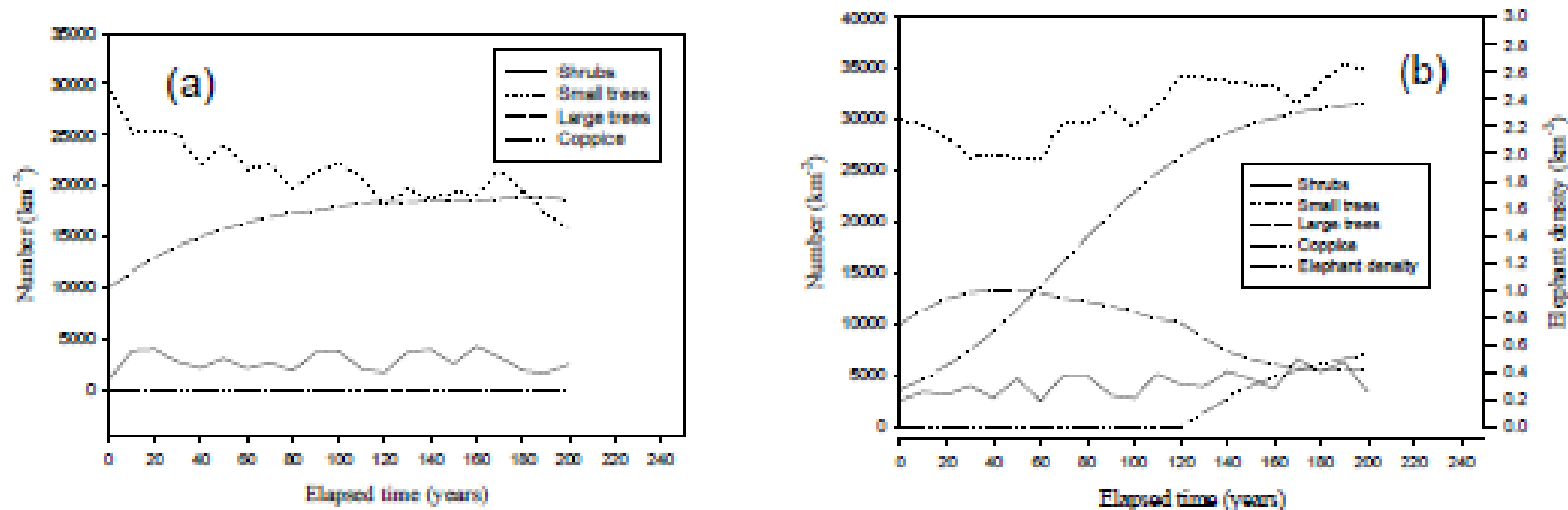
Figure 2. Initial structure (base run) of miombo woodland structure at current proportions of trees and shrubs with neither fire nor elephants (a) and changes that take place with elephant density of 0.27 km^{-2} (without culling) and no fire (b).

after 200 years, from his case study of mopane woodlands in Zambia. For any given scenario, five runs were performed. Simulations were run with randomly generated rainfall. They were run with varying combinations of elephant densities and fire frequencies. Effects of elephants and fire, applied individually or interactively, on woodland structure were monitored. For most simulations, the model was run with an initial number of 100 elephants (that is, 0.27 km^{-2}), with or without culling. In some runs, fire occurrence was set at zero and where present, it was run with a return-time of 4.7 years (Mapaure et al., 2009). The effects of fire on woody plant community structure were therefore investigated by varying the frequency of fire between annual occurrence and once in several years. Elephant densities were also varied between 0 and 2 km^{-2} to compare sensitivity of woodlands to the impacts of elephants.

RESULTS

Interactive effects of elephants and fire

Simulations clearly demonstrated changes in the structure of miombo woodland when subjected to elephants and fire. Without elephants and fire, the woodland assumed a structure characterized by well-defined proportions of the three woody strata: shrubs, small trees and large trees (Figure 2a). Since initial conditions were set at current (hence disturbed) proportions of these three strata, the figure indicates that if the two disturbance factors were removed from the system, it would take up to 120 years before stabilizing again. An initial elephant density of 0.27 km^{-2} (100 elephants) without culling and without fire, will push the system completely into a predominantly coppice woodland in about 120 years, characterised by a massive decline in large trees (Figure 2b).

The length of time before the woodland degenerates into coppice depends upon the initial density of elephants, where an elephant density of 2 km^{-2} without culling would result in conversion to coppice in about 10 years. Applying fire once in

4.7 years to the woodland, with an initial 100 Elephants without culling did not significantly change the pattern (Figure 2c). When elephants are culled at a rate of 30% when densities reach about 1 km^{-2} (starting with an initial density of 0.27 km^{-2}), the woodland does not degenerate into coppice despite the occurrence of fire once every 4.7 years (Figure 2d). The woodland would quickly establish some relatively constant proportions of the three strata.

If fire is applied alone without elephants, the woodland does not degenerate into coppice but there seems to be If fire is applied alone without elephants, the woodland does not degenerate into coppice but there seems to be an initial marked decline in the densities of small trees, apparently due to lack of shrub recruitment into small trees (Figure 2e) but trends largely remain the same as in the base run (Figure 2a). Simulations indicate that the current density of elephants estimated
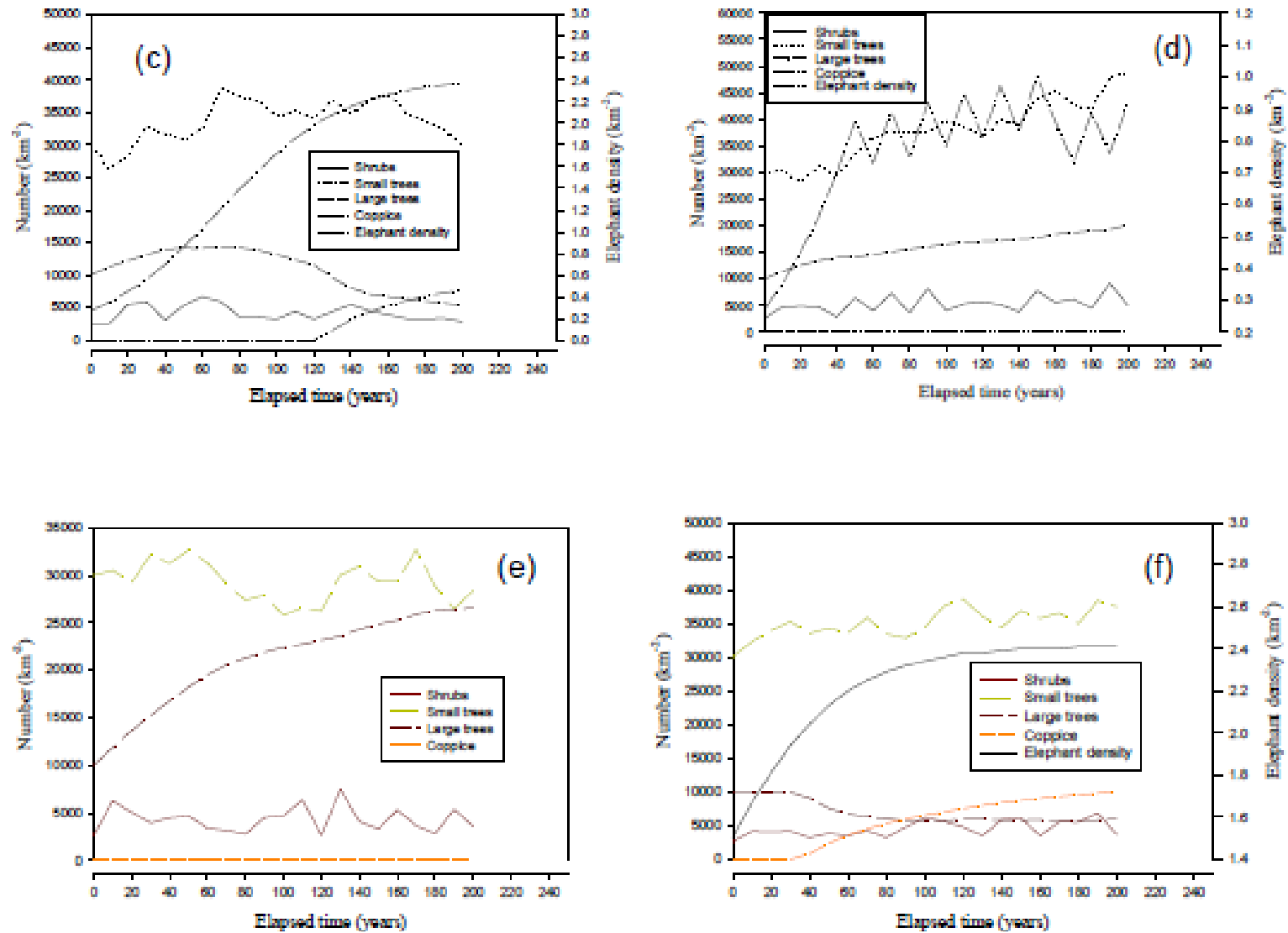
Figure 2 Contd. Initial structure (base run) of miombo woodland structure at current proportions of trees and shrubs with neither fire nor elephants. The structure in (c) shows changes when fire is applied once every 4.7 years, keeping elephant density the same (without culling). Culling elephants at 30% when their density reaches 1 km^{-2} while applying fire once every 4.7 years results in the structure shown in (d) while, (e) shows the structure of the woodland when fire is applied once every 4.7 years without elephants in the woodland. Applying an elephant density of 1.5 km^{-2} without fire results in woodland structure is shown in (f).

at 1.5 km^{-2}, if not culled, will push the woodland into coppice dominated by small trees (reversions) in 30 to 40 years (even without fire) and further deplete the coppice possibly into shrubland (Figure 2f).

Effects of varying elephant densities and fire return period

Increasing elephant densities from 0 to 2 km^{-2} resulted in small variations in the abundance of small trees at the start of the simulations but abundances increased with increase in elephant densities after about 40 years of simulations (Figure 3a). Shrubs were less affected by variations in elephant densities but showed an increase during the first 10 years (Figure 3b), which is not surprising since elephants do not have a marked direct effect on shrubs. There were sharp declines in the abundance of large trees with increases in elephant density (Figure 3c). At an elephant density of 2 km^{-2}, large trees dropped to their lowest abundance after about 60 years. This resulted in the formation of coppice woodland (Figure 3d). No coppice was formed without elephants while coppice was formed almost immediately at an initial elephant density of 2 km^{-2} without culling. An elephant density of 0.5 km^{-2} without culling will take the woodland about 100 years before degenerating into predominantly coppice. The effects of fire on trees were not evident. When fire return period was varied between non-occurrences and once in 20 years, differences in the abundance of shrubs were minimal (Figure 4a). However, the abundance of shrubs increased during the first 10 years, with increases in abundance at high fire return periods during that period.

Grazing limited the accumulation of grass fuel but this was ultimately determined by long-term rainfall patterns as evidenced by the stabilisation of the two curves in Figure 4b.

DISCUSSION

Impacts of elephants and fire

A preliminary simulation model presented in this paper has demonstrated that the impacts of elephants on miombo woodland structure were more marked than that of fire, but fire has been shown to act as a catalyst that speeds up the process through its suppression effects on woody plant recruitment into the tree layer. This situation seems to be unique to this area because of its semi-arid nature and limited grass biomass production compared to what has been reported elsewhere such as East African rangelands (Dublin et al., 1990) and various savanna woodlands of Botswana (Ben-Shahar, 1996).

However, Starfield et al. (1993) illustrated that the probability of woodland being trapped in a shrubland state increased with increasing probability of ignition. Since the major influence of fire in savanna woodlands is mainly on shrubs, it is therefore not surprising that its simulated effect on the tree layer in this model was minimal. Changes in vegetation state alluded to by Dublin et al. (1990) which can take place even in the absence of fire, confirms findings reported by Mapaure (2001) where some patches of miombo woodland had been converted to woodland-thickets in SWRA. Norton-Griffiths (1979) reported different extents to which fire may influence the process of vegetation change where some areas of the Serengeti, fires were significantly fuelled by increases in grass production due to the opening up of the canopy by elephants but in the central woodlands of the same area, fire merely tipped the balance so that the overall trend was towards a decrease in tree density.

A re-examination of hypotheses proposed by Dublin et al. (1990) implies that elephants alone are capable of degrading miombo woodlands into coppice by negatively impacting heavily on trees. Elephants are also capable of maintaining the vegetation in the new state, while fire only speeds up the process of change. It is therefore hypothesised that elephants alone can degrade semi-arid miombo woodland into coppice and can maintain it in that state, while fire only serves to accelerate the process by suppression of woody plant recruitment. Similar trends have been shown in other savanna ecosystems elsewhere (Staver and Levin, 2012).

In the model, various fire frequencies produced no major differences in woodland structure, probably due to low grass biomass production because of low rainfall, impoverished soils, as well as removal of grass fuel by wild herbivores. Gambiza et al. (2008) indicated that grazing can be very effective in reducing fire impacts on woodlands, and should be considered as a management option where reduction of fire intensity is desired. The model requires the amount of grass biomass to be above a specific value for fire to spread, but given the low rainfall regime, conditions fulfilling this requirement are often not met. Gambiza et al. (2000) indicated that removal of trees and reduction of livestock grazing caused increases in grass fuel loads resulting in a corresponding increase in fire frequency. By implication, therefore, grazing would result in low fire occurrence because of reduced fuel loads through consumption.

The occurrence of natural fires in SWRA was shown to be lower than expected (Mapaure et al., 2009), an observation supported by the model. The model also demonstrated that to maintain the current vegetation structure or to arrest its further decline into coppice, more emphasis should be put towards the management of elephant densities. Elephant densities of about 1.5 km^{-2} (possibly higher) (Mapaure and Campbell, 2002) in the area are clearly detrimental to the woodland.
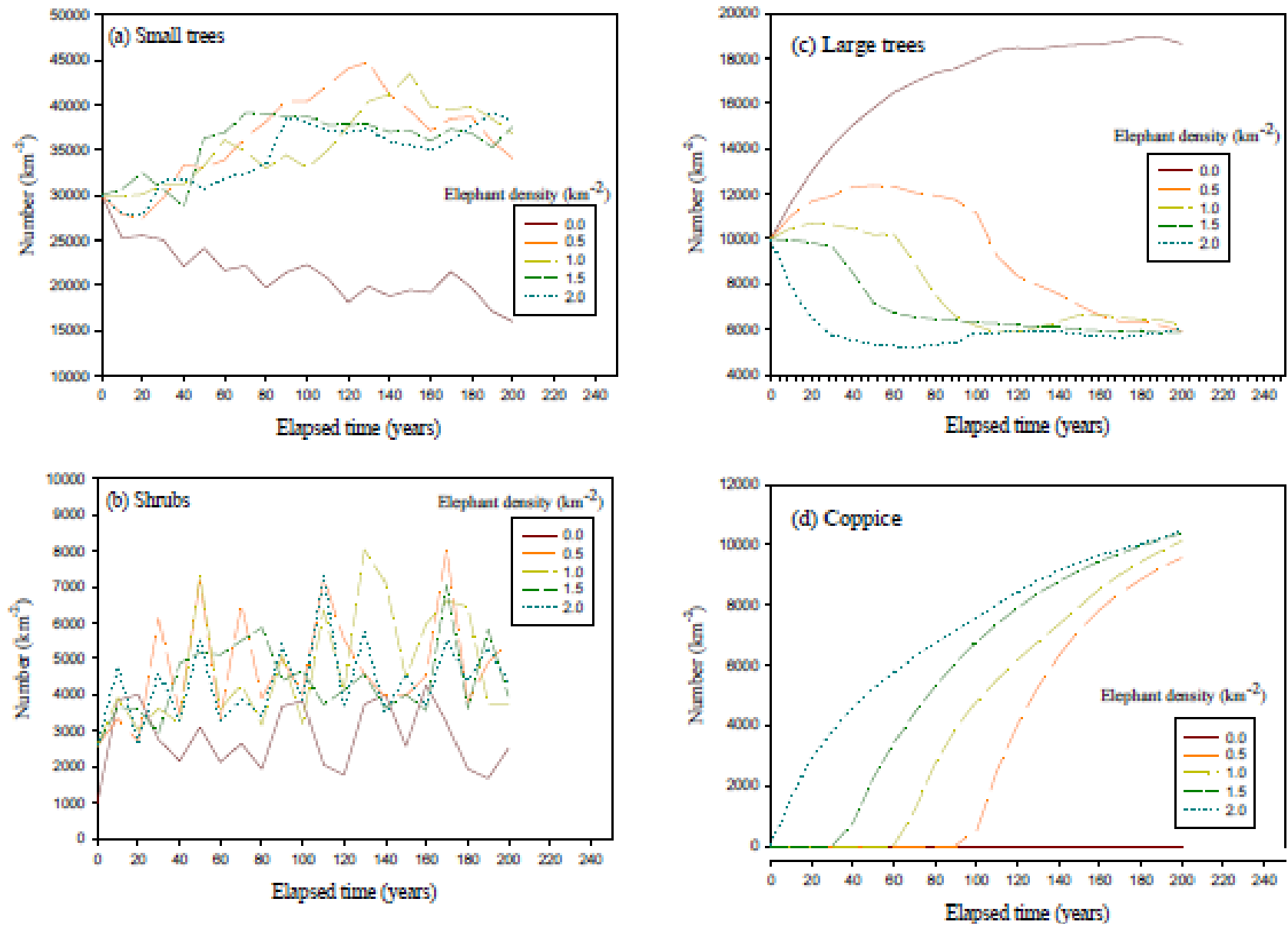
Figure 3. Changes in the abundance of small trees (a), shrubs (b), large trees (c) and coppice (d) subjected to various densities of elephants without culling and no fire occurrence.
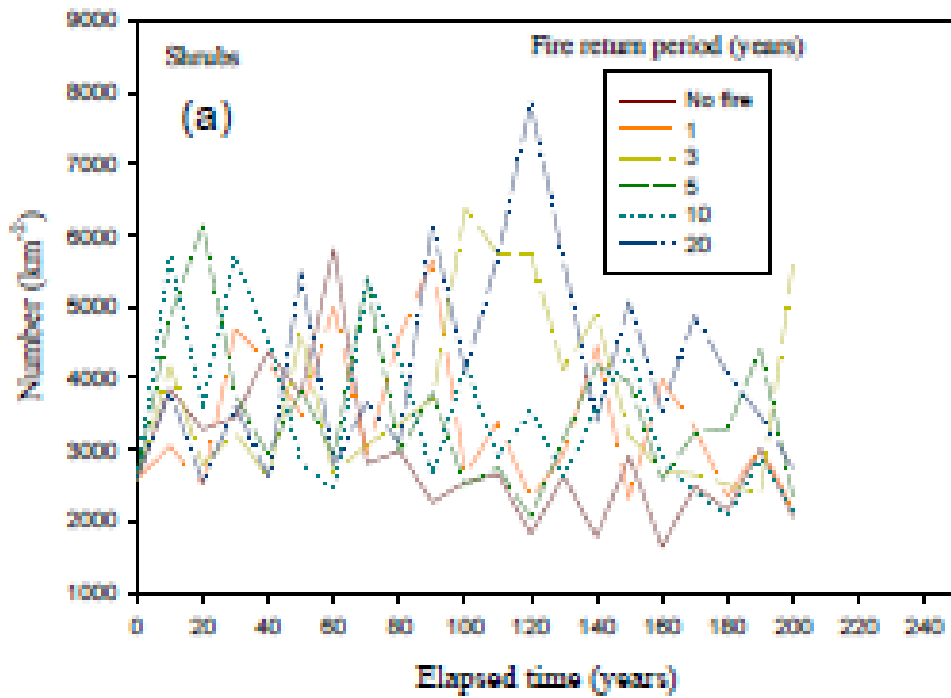
Figure 4a. Changes in the structure of the shrub layer when fire return period is varied between non-occurrence and once every 20 years, with no elephants in the woodland.
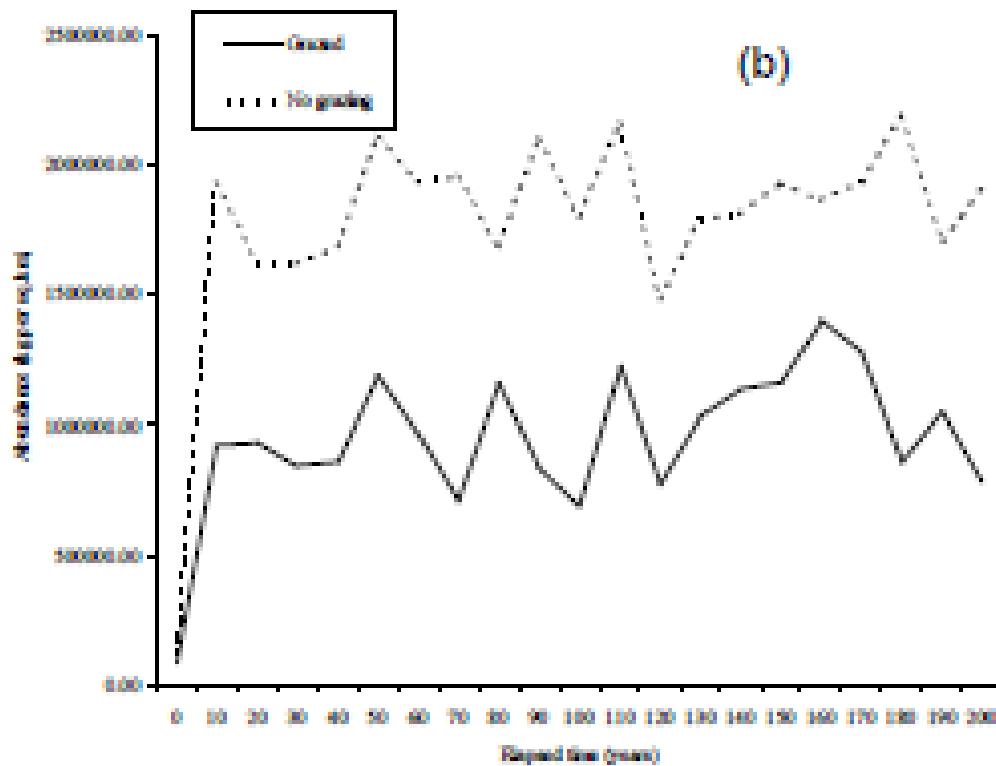

Figure 4b. Changes in the structure of the shrub layer when fire return period is varied between non-occurrence and once every 20 years, with no variations in grass fuel production in grazed and non-grazed woodland.

This observation is contrary to Baxter and Getz (2005) results which showed that at an elephant density of 1.0 km^{-2}, woody plants persisted in a Kruger National Park savanna for over a century. Therefore, caution should be exercised in applying these models as some of them may be limited to local application.

In SWRA, if elephant densities are reduced to well below 0.5 (to about 0.1) km^{-2}, the woodland may be maintained in a desirable (less degraded) state as long as the current fire management practices are maintained. Moreover, the recent transformation of the SWRA into a hunting area will have important considerations on the population structure and dynamics of the elephant populations themselves, since mostly bulls are targeted. If annual hunting quotas are known, these would have to be included in the culling factor in the simulation model. However, the changes in elephant dispersal patterns (as a result of hunting pressure) relative to the spatial distribution of the habitats would be more challenging to predict.

Future directions

Since this model deals with changes in the structure of miombo woodland based on abundances of its woody components, more insights would be derived if an element of vertical structure was built into the model. This would clearly capture the responses of the shrub layer to fire. Fire should be modeled with clear differences between early and late dry season occurrences since differences in seasonal effects of fire are well known in African savannas (Gambiza et al., 2008). Such an undertaking would pave the way to include fire intensities in the model.

An additional condition for conversion from coppice or shrub land into grassland should be built into the model. This, however, can only be possible if the model incorporates an element of floristic composition in addition to structure, which STELLA modeling may not be able to deal with since it models stocks. The overall applicability of the model beyond the study area would require some caution. Savannas are very floristically and structurally heterogenous and dynamic; hence, one would have to be cautious in generalizing this across different ecosystems.

Conclusions

Elephants alone can degrade and maintain semi-arid miombo woodland into coppice, largely due to their impacts on mature canopy trees, but fire acts to speed up the process by suppression of an already low recruitment. Fire has a lesser influence on the structure of the woodlands than elephants and does not result in degradation of miombo woodland in the area due to the low fuel loads available as a result of heavy grazing and low grass production (due to relatively low rainfall) and inhe-

rently poor soils. Fire in semi-arid miombo woodland does not necessarily lead to an increase in densities of shrubs but would certainly lead to height reversions. Current elephant densities in SWRA may degrade the ecosystem into predominantly coppice woodland in less than 40 years and should, therefore, be reduced to about 0.1 km^{-2} [which seems to be within the carrying capacity of (at least) the miombo ecosystem]. Recent introduction of hunting in the area may help to reduce the elephant populations to manageable densities or to keep their population under control, depending on the annual quotas set for hunting.

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Appendix. The five interactive sub-models built in STELLA showing rainfall sub-model (a), grass sub-model (b), fire sub-model (c), elephant sub-model (d) and tree sub-model (e).
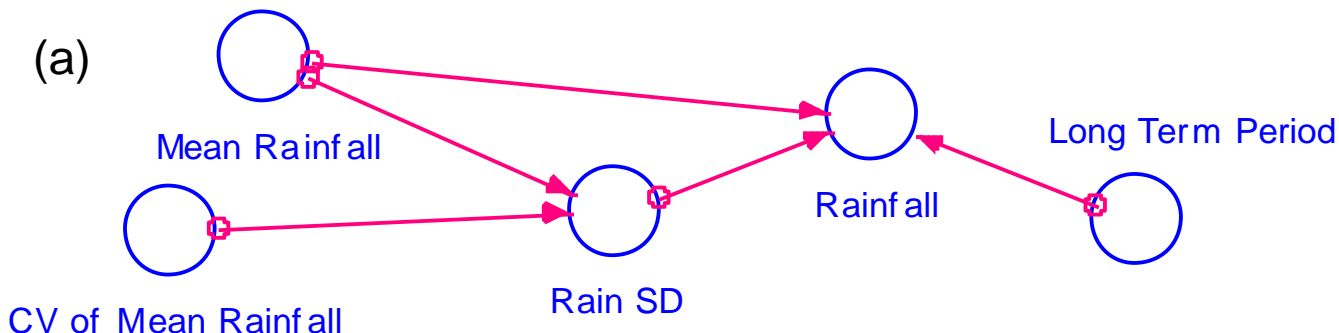
CV_of_Mean_Rainfall = 0.26.
The standard deviation of rainfall for SWRA for the period of 1965/1966 to 1996/1997 is 165.7 mm. This gives a coefficient of variation of 25.8%. This parameter is used here to adjust the standard deviation of the mean rainfall when mean rainfall is varied (auxiliary variable RAIN_SD.).

Long_Term_Period = 20.
Rainfall in the summer rainfall area of southern Africa shows quasi-periodicity with a cycle length of approximately 20 years, with about 10 years of above-average rainfall alternating with 10 years below-average rainfall (Tyson, 1986).

Mean_Rainfall = 642 mm p.a.
The mean annual rainfall for SWRA for the period of 1965/1966 to 1996/1997 is 641.9 mm (unpublished data at SWRI internal files). This rainfall amount sets the basic level of rainfall for Gokwe South, NW Zimbabwe, but it can be varied to simulate other rainfall conditions.

Rainfall = NORMAL(Mean_Rainfall, Rain_SD) + 0.1*Mean_Rainfall*SINWAVE(1,Long_Term_Period).
This is a rainfall generator that takes into account periodicity in rainfall (long-term period = 20 years). Annual rainfall is a random variable drawn from a normal distribution defined by the mean annual rainfall and standard deviation. The amplitude of the long-term periodicity is set at 10% of the mean annual rainfall. This is in turn scaled to 1 within the sine wave function.

Rain_SD = Mean_Rainfall*CV_of_Mean_Rainfall.
This variable is calculated as the product of Mean_Rainfall and CV_of_Mean_Rainfall. The standard deviation of mean rainfall therefore varies as a function of mean rainfall, thus allowing mean rainfall to be varied in a consistent manner.
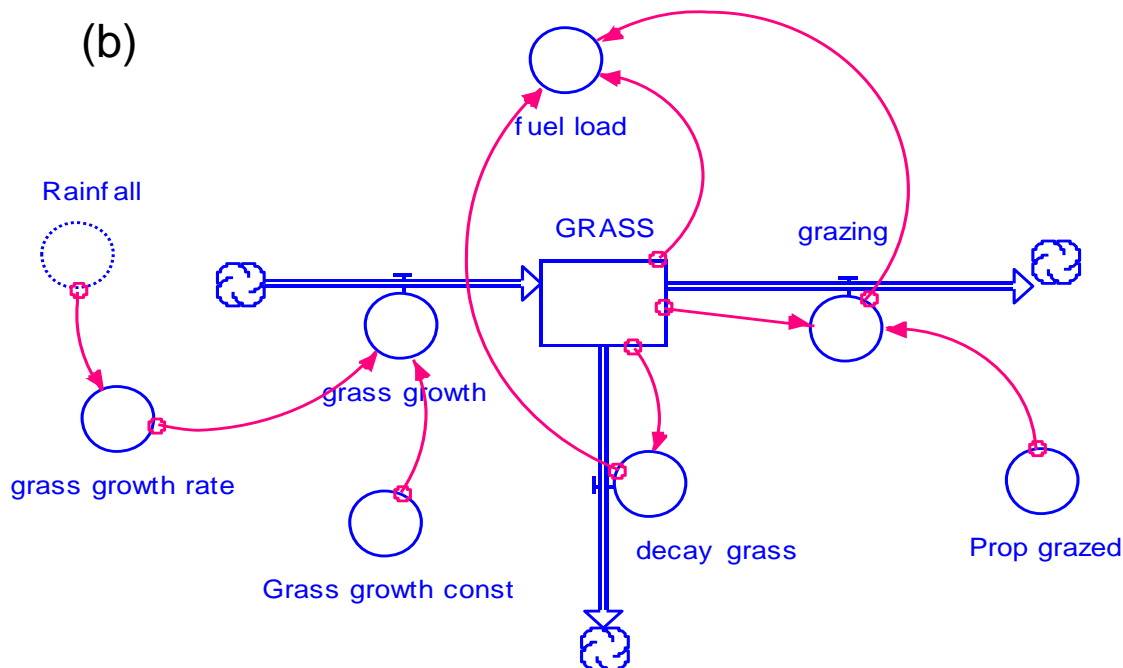
GRASS(t) = GRASS(t - dt) + (grass_growth - decay_grass - grazing) * dt.

INIT GRASS = 200000 kg.
Initial grass biomass. Maximum biomass at Samapakwa in SWRA was 186000 kg km^{-2}; hence, initial biomass set at 200000. Maximum set at 300000 for complete grassland.
grass_growth = grass_growth_rate*Grass_growth_const.

decay_grass = GRASS*EXP(-0.88).
This flow reduces grass biomass through decay. The grass decay rate (k = -0.88 yr^{-1}) is derived from Frost (1996:38), though note that this value comes from a litter bag experiment carried out at Marondera, Zimbabwe (MAP = 885 mm p.a.), not from measurements of the decay of standing grass in a drier environment. Equation relating the decay rate (K) to grass biomass (F) is: Ft = Fo*Exp(-Kt) (Scholes et al., 1996).

grazing = GRASS*Prop_grazed.
This flow reduces grass biomass as a function of grazing pressure, itself a product of grass biomass and grazing rate.

fuel_load = GRASS-(grazing+decay_grass).
Grass biomass less grazing and decay (= fuel load).

Grass_growth_const = 1000.
Constant adjusts for effects of shading, etc, that also limit grass growth. This is the minimum amount of grass per km^2 generated with the lowest rainfall received in the area.

grass_growth_rate = 2*Rainfall.
1 mm rain produces 2 kg ha^{-1} of grass on sandy soils. Dye and Spear (1982).(= 200 kg km^{-2}). 1 mm rain produces 1 kg ha^{-1} under a heavy canopy (Frost, 1996). Scholes et al. (1996) give a figure of 1.25 kg ha^{-1} for all infertile savannas.

Prop_grazed = 0.15.
This proportion has been set as a function of amount of graze available rather than the stocking rate since it is a bit difficult to calculate stocking rate in livestock units for a multispecies system.

(c)
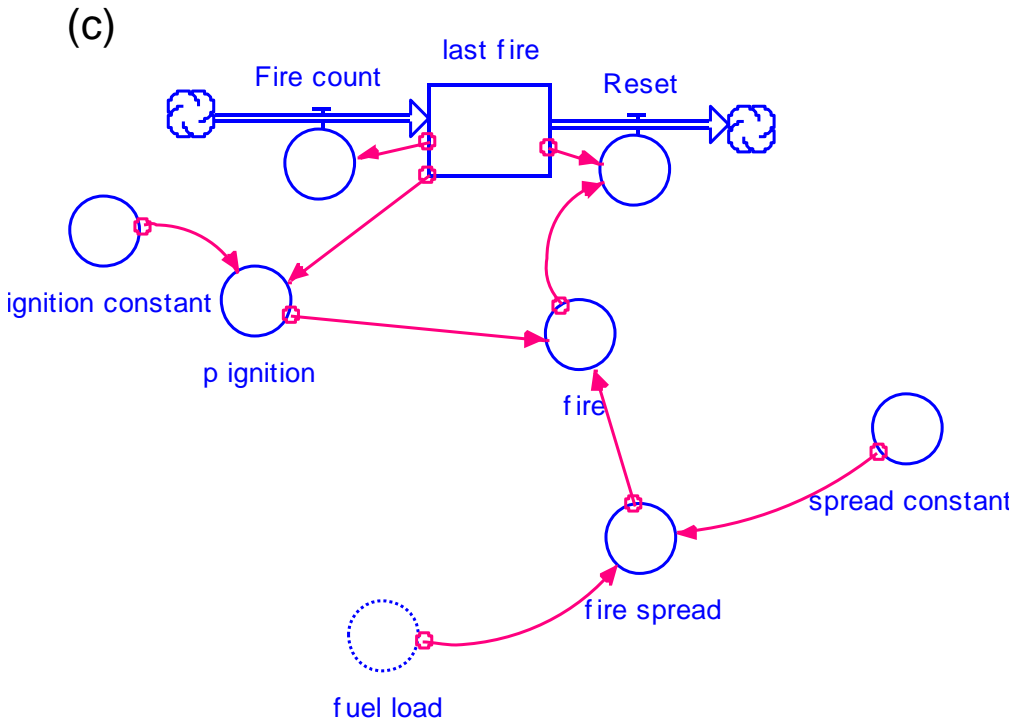
last_fire(t) = last_fire(t - dt) + (Fire_count - Reset) * dt.

INIT last_fire = 4.7.
Fire return period in the area (Mapaure et al., 2009).

Fire_count = 1-EXP(-(dt/last_fire)).
The distribution function of Fire return interval (T) is given by F(t) = 1-exp(-t/y) (Polakow and Dunne, 1999; Johnson and Gutsell, 1994).

Reset = if fire = 1 then (last_fire/dt) else 0.

fire = if(fire_spread > 0) then(fire_spread*p_ignition) else (0).

fire_spread = if fuel_load > spread_constant then 1 else 0.

ignition_constant = 0.3.

p_ignition = (1- (1/last_fire))*ignition_constant.
Relationship derived from the Weibull equation given by Polakow and Dunne (1999:87). Note - Probability of ignition without management fires in SWAR is 0.32 (Mapaure et al., 2009).

spread_constant = 800 kg ha^{-1}.

800 kg ha^{-1} minimum needed to get a fire spreading (Stronach and McNaughton, 1989; Scholes et al., 1996) (= 5000 kg km^{-2}).

(d)
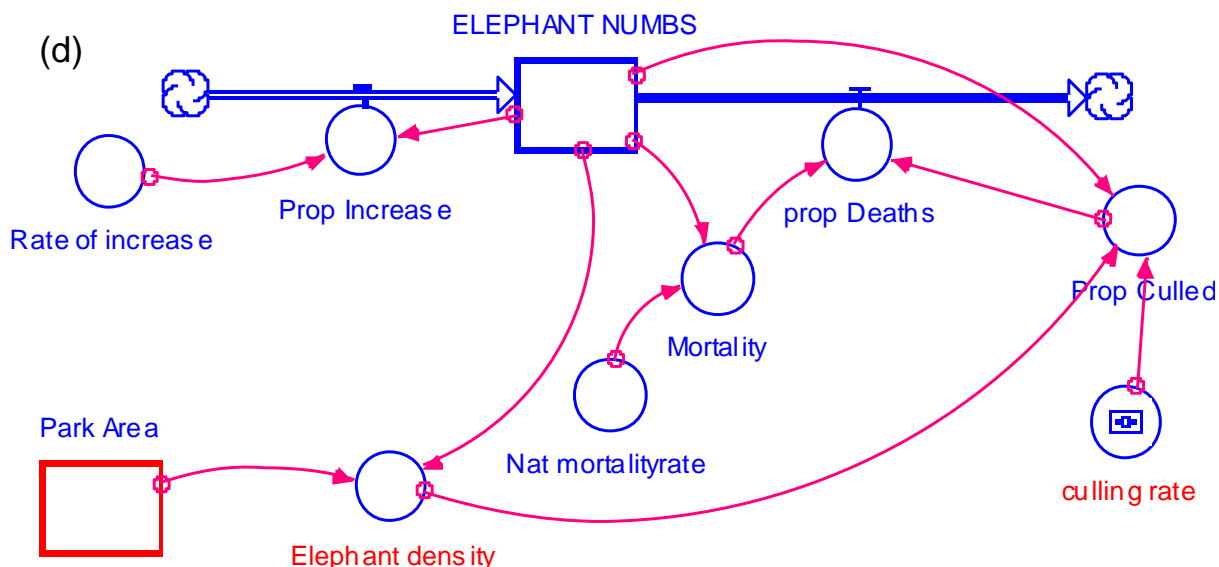
ELEPHANT_NUMBS(t) = ELEPHANT_NUMBS(t - dt) + (Prop_Increase - prop_Deaths) * dt.

INIT ELEPHANT_NUMBS = 100.
The maximum elephant density at which no adverse effects on vegetation are caused. Guy (1989) indicated an upper limit of 250 elephants in 373 sq. km.

Prop_Increase = Rate_of_increase*ELEPHANT_NUMBS*((1500-ELEPHANT_NUMBS)/1500).
This is the logistic growth equation indicating an upper limit (K, carrying capacity) of 1500 elephants for the whole of SWRA.

prop_Deaths = Prop_Culled+Mortality.
Sum of culling proportion and natural mortality scaled by density. This gives total elephant deaths.

Park_Area(t) = Park_Area(t - dt).

INIT Park_Area = 373.

culling_rate = 0.3 (when switched on).

Elephant_density = (ELEPHANT_NUMBS)/(Park_Area).

Mortality = ELEPHANT_NUMBS*Nat_mortalityrate.

Nat_mortalityrate = 0.02.
The propotion of elephants that die of causes other than culling. This has been set low at 0.02 (that is 2% per annum). This is the average derived from mortality of 1.2% in 1989, 2.4% in 1994 and 2.4% in 1995 (DNPWLM, 1996) (Note: figures were records of carcases; hence, may include poached animals since there was no distinction made).

Prop_Culled = IF(Elephant_density >1)THEN (ELEPHANT_NUMBS*culling_rate)ELSE(0).

Rate_of_increase = 0.05.

Intrinsic growth rate of elephant populations. Cumming et al. (1997) reported an increase of 5% per annum in Zimbabwe and Armbruster and Lande (1993) reported an increase of 5% per annum in Tsavo, Kenya. These figures are LESS (minus) mortality. Hence, actual additions before accounting for mortality are higher than these. Gibson (1983) reported increases of 4.19 and 3.79% per annum in SWRA; hence, the average 4.5% has been used.

(e)
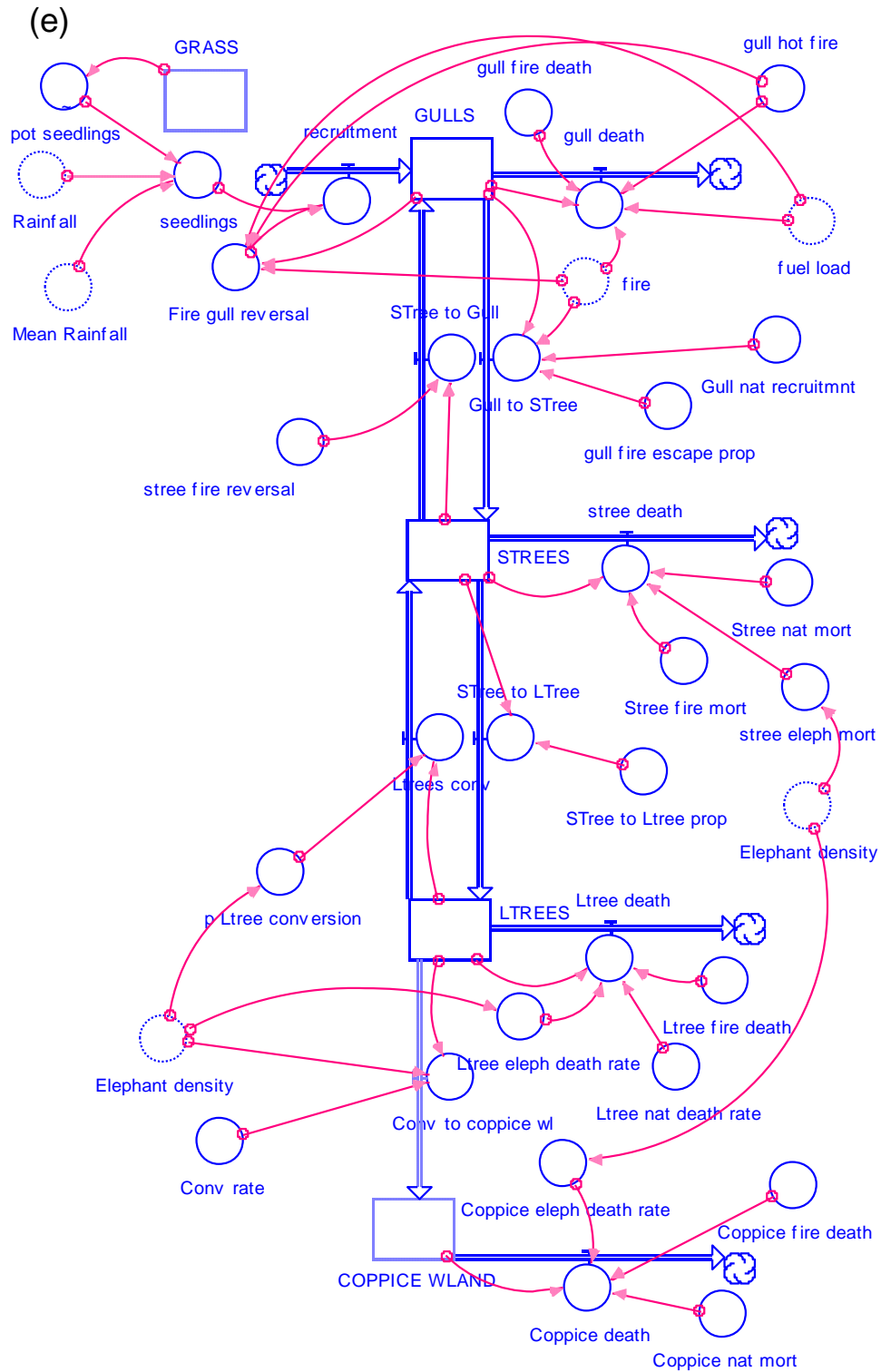
COPPICE_WLAND(t) = COPPICE_WLAND(t - dt) + (Conv_to_coppice_wl - Coppice_death) * dt.

INIT COPPICE_WLAND = If (Conv_to_coppice_wl>0)then(Conv_to_coppice_wl*LTREES)else 0.
Conv_to_coppice_wl = IF Elephant_density >2 THEN (Conv_rate*LTREES) ELSE(0).
Proportion of trees converted to shrubland. This change of state can only take place when elephant numbers are above 250 per km^{-2}; hence, can only take place if product of conversion rate and elephant numbers (that is, 0.11*250) is above this level, otherwise no conversion to different state takes place.

Coppice_death = COPPICE_WLAND*(Coppice_eleph_death_rate+Coppice_fire_death+Coppice_nat_mort).
GULLS(t) = GULLS(t - dt) + (recruitment + STree_to_Gull - Gull_to_STree - gull_death) * dt.
INIT GULLS = 1000.
recruitment = seedlings+Fire_gull_reversal.
This assumes that the number recruited into the gull stage is the sum of the number of seedlings (cf seedling rule) and the number of resprouts produced by elephant-felled trees from both the small and large trees (the proportions of resprouts have been set at a low rate).

STree_to_Gull = STREES*stree_fire_reversal.

Gull_to_STree = if(fire = 1) then (gull_fire_escape_prop*GULLS) else GULLS*Gull_nat_recruitmnt.
An estimated proportion of gullivers/shrubs that get above 2 m.

gull_death = if(fire = 1) and (fuel_load > gull_hot_fire) then (gull_fire_death*GULLS) else (0).
Total number of gullivers that die from various reasons.

LTREES(t) = LTREES(t - dt) + (STree_to_LTree - Ltree_death - Ltrees_conv - Conv_to_coppice_wl) * dt.

INIT LTREES = 10000.
Trees > 20 cm dbh. About 25% of trees are in this category (Mapaure and Moe, 2009). Taking an initial tree density of 400 trees/ha (40000/sq. km), then there are 10000 trees/sq. km in this category.

STree_to_LTree = STree_to_Ltree_prop*STREES.
Refers to the number of Strees that grow to Ltrees. This was assumed to take 15 years and was scaled by the maximum woody basal area. Calculated as the product of the proportion of Strees that grow into Ltrees and the reciprocal of the number of years taken to mature, scaled by basal area.

Ltree_death = LTREES*(Ltree_nat_death_rate+Ltree_eleph_death_rate+Ltree_fire_death).
Estimated tree longevity is 200 years. Fire assumed to have no detrimental effect on large trees.

Ltrees_conv = LTREES*p_Ltree_conversion.
Proportion of Ltrees converted to Strees by elephant herbivory.

Conv_to_coppice_wl = IF Elephant_density>2THEN(Conv_rate*LTREES) ELSE(0).
Proportion of trees converted to shrubs and/coppice. This change of state can only take place when elephant densities exceeded 2 km^{-2}); hence, can only take place if product of conversion rate and elephant numbers (that is, 0.11*250) is above this level, otherwise no conversion to different state takes place.

STREES(t) = STREES(t - dt) + (Gull_to_STree + Ltrees_conv - stree_death - STree_to_Gull - STree_to_LTree) * dt.

INIT STREES = 30000.
Trees 2 to 5 m tall. 75% of total trees is in this category, while the remainder is in the large tree category. Initial overall density is 40000 trees km^{-2} (present study).

Gull_to_STree = if (fire = 1) then (gull_fire_escape_prop*GULLS) else GULLS*Gull_nat_recruitmnt.
An estimated proportion of gullivers/shrubs that get above 2 m.

Ltrees_conv = LTREES*p_Ltree_conversion.
Proportion of Ltrees converted to Strees by elephant herbivory.

stree_death = STREES*(stree_eleph_mort+Stree_fire_mort+Stree_nat_mort).
Estimated about 3% die each year.

STree_to_Gull = STREES*stree_fire_reversal.

STree_to_LTree = STree_to_Ltree_prop*STREES.
Refers to the number of Strees that grow to Ltrees. This was assumed to take 15 years.

Conv_rate = 0.021.
There was a loss of 1.1% of vegetation cover (Mapaure and Campbell, 2002). This has been taken to translate into change in state but above a critical elephant density (conv to shrubland). Calculations from damage assessments (Mapaure and Moe, 2009) give conversion at 2.1% per year.

Coppice_eleph_death_rate = 0.00015*Elephant_density.

(conversion rate for L-trees).

Coppice_fire_death = 0.006.
Fire becomes important again here (as opposed to Ltrees) and kills similar proportions as gullivers/shrubs.

Coppice_nat_mort = 0.0038.
Coppice death in the absence of elephants. (Ltrees nat mortality).

Fire_gull_reversal = IF(fire = 1)AND(fuel_load>gull_hot_fire)THEN(0.30*GULLS)ELSE(0).
The proportion of shrubs reversed by fire (that is, 1-(fire escape+fire mort+shade mort). Ben Shahar (1996) recorded 70% fire reversal in new seedlings and 31% fire reversal in shrubs in *Baikiaea* woodland.

gull_fire_death = 0.015.
The proporiton of gullivers that die in a fire. Present study shows that 3.1% (= 0.031) died (Mapaure, in press) after two fires/2 years (and 1.1% had died after one fire). Hence, mortality was 1.5% per year (0.015).

gull_fire_escape_prop = 0.1.
Mapaure and Moe (2009) have shown an increase in small tree proportions equivalent to 2.5% per year, implying similar net recruitment rate. But this was inclusive of other influences. Hence, actual escape rates may even be twice this figure since fire is patchy.

gull_hot_fire = 1000.
This is a constant referring to the minimum fuel load required for a fire to kill 10% of the gullivers. It was set at 1000 kg DM per ha. [Trollope (1993) found out that fire can only spread in savannas at grass fuel >1000 kg DM/ha; fires as low as 800 kg DM/ha do not cause top-kill of gullivers (Rushworth, 1975)].

Gull_nat_recruitmnt = 0.3.

Ltree_eleph_death_rate = Elephant_density*0.00015.
Elephant- induced death rate of large trees. This is a function of the number of trees available and the elephant density. In SWRA, each elephant pushes down 1500 trees per year (Cumming, 1981) and I assumed that a large proportion of pushed down trees dies (which is not always true). The original number of trees has been incorporated into the calculation because availability of trees is likely to affect the number of trees pushed down per elephant per year. The proportion is therefore 1500/10000 (= 0.15). But Sharp (1982) reported that trees were being lost at 9% per year at about 1.6 elephants km^{-2} (that is, 1 elephant km^{-2} accounts for 5.63%, = 0.00015 elephant/tree year (Duffy et al., 1999) gave range 5.9 to 7.5×10^{-6}).

Ltree_fire_death = 0.
Negligible numbers of trees killed by fire.

Ltree_nat_death_rate = 0.01.
Large tree mortality in the absence of elephants (for example, caused by drought, old age). Bond and van Wilgen (1996) gave 0.38%. In SWRA, this could be much lower than this per year.

p_Ltree_conversion = Elephant_density*0.013.
Tree height reduction over 16 years was 2.1% per year, at an average elephant density of 1.6 km^{-2} (Mapaure and Moe, 2009). Hence, conversion factor is 1.3% per elephant per sq. km.

seedlings = if Rainfall>Mean_Rainfall*1.25 then pot_seedlings else 0.
This assumes that we only get seed production in above average rainfall years and that grass biomass influences how many seedlings establish (as gulls). Seedling production is therefore independent of the total number of trees producing seed in the stand - this is because it is assumed that seed production is non-limiting. Perhaps, we should be able to switch seed production off when the number of small trees and large trees gets below a critical level.

stree_eleph_mort = 0.0001*Elephant_density.
The proportion of small trees that are killed by elephants. About a 1.3% (that is, 0.01) per annum loss in small trees was recorded (Mapaure and Moe, 2009). Norton-Griffiths (1979) reported a 1% mortality in Serengeti.

Stree_fire_mort = 0.001.
The proportion of small trees that are killed by fire. As most trees survive the fire, this constant has been set at a very low rate. Note: 28% of trees in 2 to 3 m height class were burnt back but not necessarily killed (Norton-Griffiths, 1979). Bond and van Wilgen (1996) give 0.63% (0.006 prop) and 1.58% for early and dry season fires, respectively. Again this is much lower (than 0.0063) in SWRA because of patchy fires.

stree_fire_reversal = 0.028.
The proportion of small trees that are reversed by fire. Observations from Serengeti indicate that tree survival from fire was 8, 32, and 72% in three height classes of the trees affected and that fire does not affect trees larger than 3 m in height (Norton-Griffiths, 1979). In SWRA, however, the proportion is very low (100 minus 72). Ben Shahar (1996) reported fire reversal rate on trees of 28% in *Baikiaea* woodland. Since the fires are very patchy in SWRA, his figure could be more than 10 times that of SWRA.

Stree_nat_mort = 0.004.
It is assumed that natural mortality in small trees (2 to 5 m) is negligible (Norton-Griffiths, 1979). (0.38%) (Bond and van Wilgen, 1996).

STree_to_Ltree_prop = 0.01.
The proportion of small trees that recruit into large trees each year.